

Natural Versus Anthropogenic Dispersal of Freshwater Turtles Between the Baja California Peninsula and Mainland Mexico

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Abstract

Trachemys nebulosa is a freshwater turtle found on the Baja California Peninsula (BCP) and mainland northwestern Mexico. Two subspecies are recognized: *Trachemys nebulosa nebulosa* from the BCP and *Trachemys nebulosa hiltoni* from the mainland. Previous genetic studies found small differences between these taxa, but limited sampling left questions about their distinctiveness and origins. Most authors who have studied this species have invoked human-mediated transport to explain its distribution. To test this hypothesis, we combined previously published genetic data with expanded sampling. Mainland and peninsular populations did not share mitochondrial or nuclear sequences, and data from both genomes separated them into distinct groups. These results support retaining *T. n. hiltoni* and *T. n. nebulosa* as separate taxa and favor a natural dispersal from the BCP to the mainland, followed by isolation of mainland populations. Because *T. n. hiltoni* has a limited distribution and is harvested for food, recognizing it as a distinct lineage has conservation implications. Additional sampling, particularly from the Cape Region of the BCP, will help further test historical connections between mainland and peninsular populations.

Keywords: biogeography; dispersal; freshwater; phylogeography; translocation; *Trachemys*; *Trachemys nebulosa*; *Trachemys nebulosa hiltoni*

1. Introduction

The evolutionary specializations of turtles, including their iconic shells and durability, helped them survive for hundreds of millions of years, through multiple mass extinctions. Unfortunately, these traits provide little defense against humans. Species of the genus *Homo* have consumed turtles since before the origin of *Homo sapiens* [1]. As human populations expanded, exploitation and habitat modification caused major declines in turtle populations. As a result, turtles are now among the most imperiled groups of vertebrates [2]. Ironically, turtles' durability made them an ideal survival food for voyaging humans. This led to preferential harvesting that supported prehistoric migrations [3,4], the European colonization of the Americas [5,6], and the whaling industry [6,7].

This long history of human use is reflected in genetic studies documenting numerous turtle translocations [8–15]. Distinguishing natural from anthropogenic distributions informs conservation, as non-native populations generally have lower conservation value.



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One unresolved case is the Mexican species *Trachemys nebulosa*, which includes two putative subspecies on either side of the Gulf of California: (1) *Trachemys nebulosa nebulosa*, the Baja California Slider, and (2) *Trachemys nebulosa hiltoni*, the Fuerte Slider (Figure 1) [16].

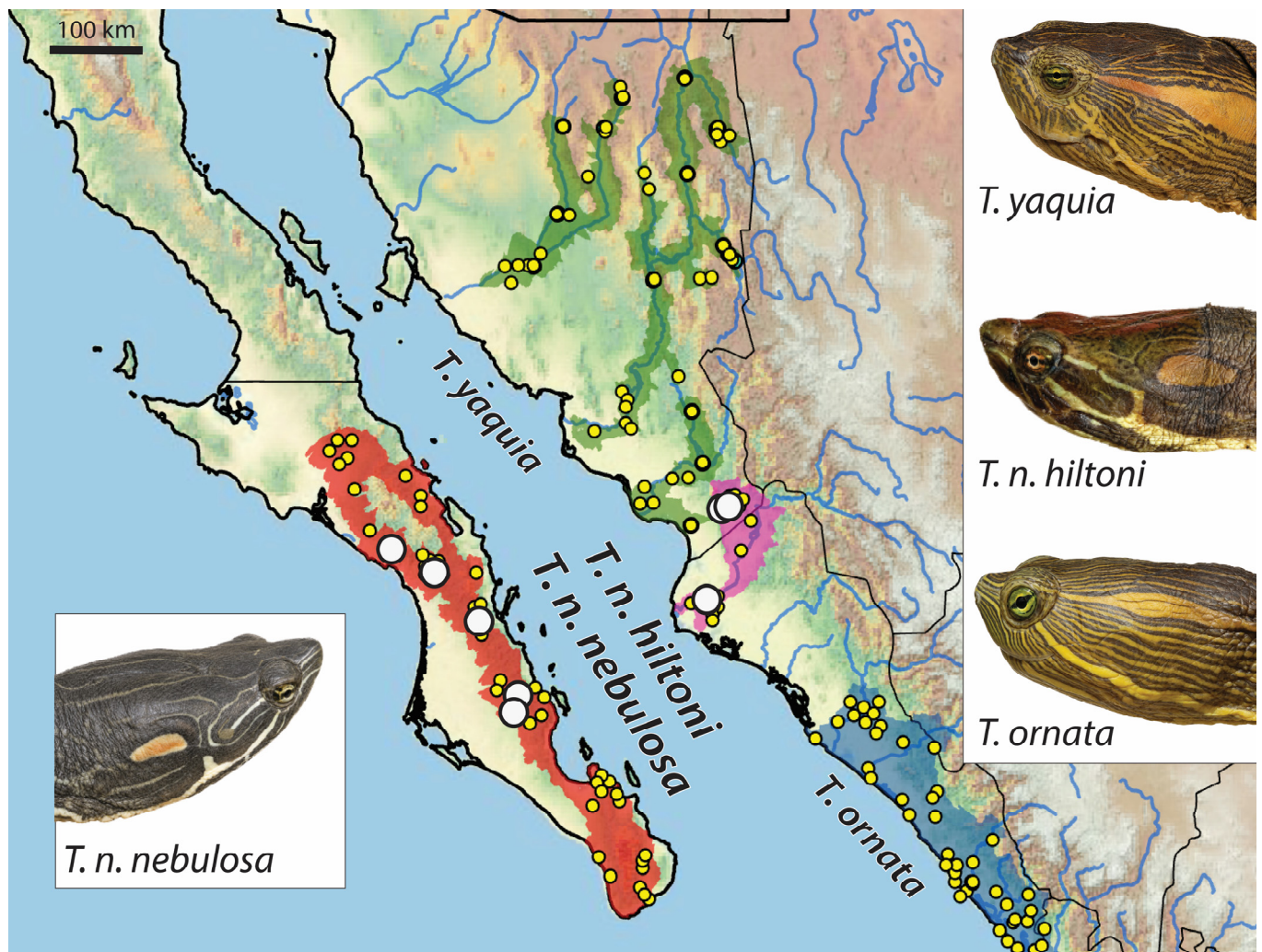


Figure 1. Distribution of *Trachemys* taxa in northwestern Mexico. The distribution of *T. n. nebulosa* is shown in red, *T. n. hiltoni* in pink, *T. yaquia* in green, and *T. ornata* in blue. Enlarged white and black circles indicate localities of samples included in the genetic analyses, and yellow circles indicate historic records. Head illustrations show representative coloration and head pattern morphology for *T. yaquia*, *T. n. hiltoni*, *T. ornata*, and *T. n. nebulosa*. The basemap, including historic records, was modified from [16], provided by Anders Rhodin, and reproduced with permission.

Trachemys nebulosa is a large, omnivorous, basking freshwater turtle primarily associated with permanent freshwater habitats [17,18]. It remains unclear whether the species originated on the mainland [19,20] or on the Baja California Peninsula (BCP) [17,21], but most authors have invoked the possibility of human-mediated transport to explain its distribution [17,19–22]. This hypothesis is plausible because the morphological differences are subtle [21,22], and historical human connections between the peninsula and the mainland may have facilitated their translocation [22,23].

Determining whether populations of *Trachemys nebulosa* are native or introduced is important because *T. n. hiltoni* has one of the smallest distributions of any continental North American *Trachemys*, exceeded only by *Trachemys venusta taylori* [21,24,25] making it vulnerable to ongoing harvest for food [18]. However, if mainland populations of

T. n. hiltoni arose through human introductions from the BCP, their conservation value may be lower than that of the endemic *T. nebulosa* populations on the BCP.

Although not the primary focus of previous studies, genetic studies of Mexican *Trachemys* provided preliminary tests of the distinctiveness of *T. n. nebulosa* and *T. n. hiltoni* [12,21]. In those studies, a single sample of *T. n. nebulosa* differed slightly from samples of *T. n. hiltoni*, which is consistent with retaining the two as separate taxa. However, the results are inconclusive due to limited sampling. We combine available genetic data for *T. nebulosa* with expanded sampling to test the distinctiveness and origins of its subspecies.

2. Materials and Methods

Total genomic DNA was extracted from liver using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany). We generated sequence data from 18 samples of *T. nebulosa* (11 *T. n. nebulosa*, seven *T. n. hiltoni*) and five outgroup *Trachemys*: *T. gaigeae*, *T. hartwegi*, *T. ornata*, *T. venusta cataspila*, and *T. venusta taylori* (Table S1). The samples are housed in museum collections and were obtained as museum loans (Table S1). Some of these specimens had been sequenced in a previous study [12] but were resequenced here to obtain longer, higher-quality reads. Homologous mitochondrial (mt) DNA sequences for all available *T. n. nebulosa* and *T. n. hiltoni*, multiple members of the *T. venusta* complex, all remaining nominal species of *Trachemys*, and the outgroup *Malaclemys terrapin* were downloaded from GenBank (Table S1 [26]). *Malaclemys terrapin* was chosen as the outgroup following a recent study [21] that identified it as the closest mitochondrial relative of *T. nebulosa*, possibly as the result of an ancient mitochondrial capture event. Our mtDNA sampling includes data from 26 museum specimens of *T. nebulosa* (12 *T. n. nebulosa*, 14 *T. n. hiltoni*) and 21 representatives of other *Trachemys* species (Figure 2). Museum voucher numbers for all specimens are provided in the Supplementary Materials (Table S1). One fragment of mtDNA and three fragments of nuclear (nu) DNA were amplified and sequenced from the extractions. An 884-nucleotide base pair (bp) fragment of mtDNA that encodes part of the NADH dehydrogenase subunit 4 gene, the complete tRNAs histidine and serine, and part of the tRNA leucine (hereafter ND4) was amplified by the polymerase chain reaction (PCR) at annealing temperature (T_m) 58 °C using the primers L-ND4 and H-Leu [27]. A 934 bp fragment of nu DNA encoding intron 2 of the hepatocyte nuclear factor 1 α (HNF-1 α) gene was amplified at T_m 62 °C using the primers HNFAL-F and HNFAL-R [28]). A ca. 1200 bp fragment of nu DNA encoding intron 61 of the reelin (RELN) gene was amplified at T_m 61 °C using the primers RELN61F and RELN61R [29]. A 1125 bp fragment of nu DNA encoding intron 1 of the RNA fingerprint protein 35 (R35) gene was amplified at T_m 58 °C using the primers R35Ex1 and R35Ex2 [30]. PCR products were cleaned using ExoSAP-IT (Thermo Fisher Scientific, Waltham, MA, USA) and sequenced in both directions by direct double-strand cycle sequencing using the BigDye Terminator version 3.1 Cycle Sequencing Kit and the amplifying primers on a 3130 DNA Analyzer or 3500xl DNA Analyzer (all products by Applied Biosystems, Foster City, CA, USA). The internal primers L-ND4intEmys and H-ND4intEmys [11] were also used in the ND4 sequencing reactions, and the internal primers L-R35int and H-R35int [31] were also used in the R35 sequencing reactions. Sequences were edited using Geneious Prime 2025.1.2 (Dotmatics, Boston, MA, USA) and deposited in GenBank under accession numbers PZ694204–PZ694280 (Table S1).

Newly generated and downloaded sequences were aligned using the default parameters in the MAFFT 7.490 alignment algorithm (Osaka University, Osaka, Japan) [32] implemented in Geneious Prime 2025.2.1 (Dotmatics, Boston, MA, USA). The alignment was trimmed to the length of the newly generated sequences (884 bp) and visually inspected to ensure that insertions and deletions did not disrupt the translation of the coding regions. The dataset was partitioned by tRNA and codon positions of ND4. The best-fit partitioning

scheme and sequence evolution models were selected using the Akaike Information Criterion (AICc) in PartitionFinder 2 (Australian National University, Canberra, Australia) [33]. Three partitions were selected: GTR + G for tRNA and the ND4 first codon position combined; GTR + I + G for the ND4 second codon position; and GTR + G for the ND4 third codon position. Maximum likelihood (ML) analysis was performed on the partitioned dataset using RAXMLGUI 2.0.16 (Antonelli Lab, Gothenburg Global Biodiversity Centre, Gothenburg, Sweden) [34]. The GTR + I + G model was applied to the three partitions selected by PartitionFinder 2 in a single analysis. Node support values were estimated by the thorough bootstrap (BS) with 500 pseudoreplicates. Nodes with bootstrap (BS) values ≥ 90 were considered statistically supported.

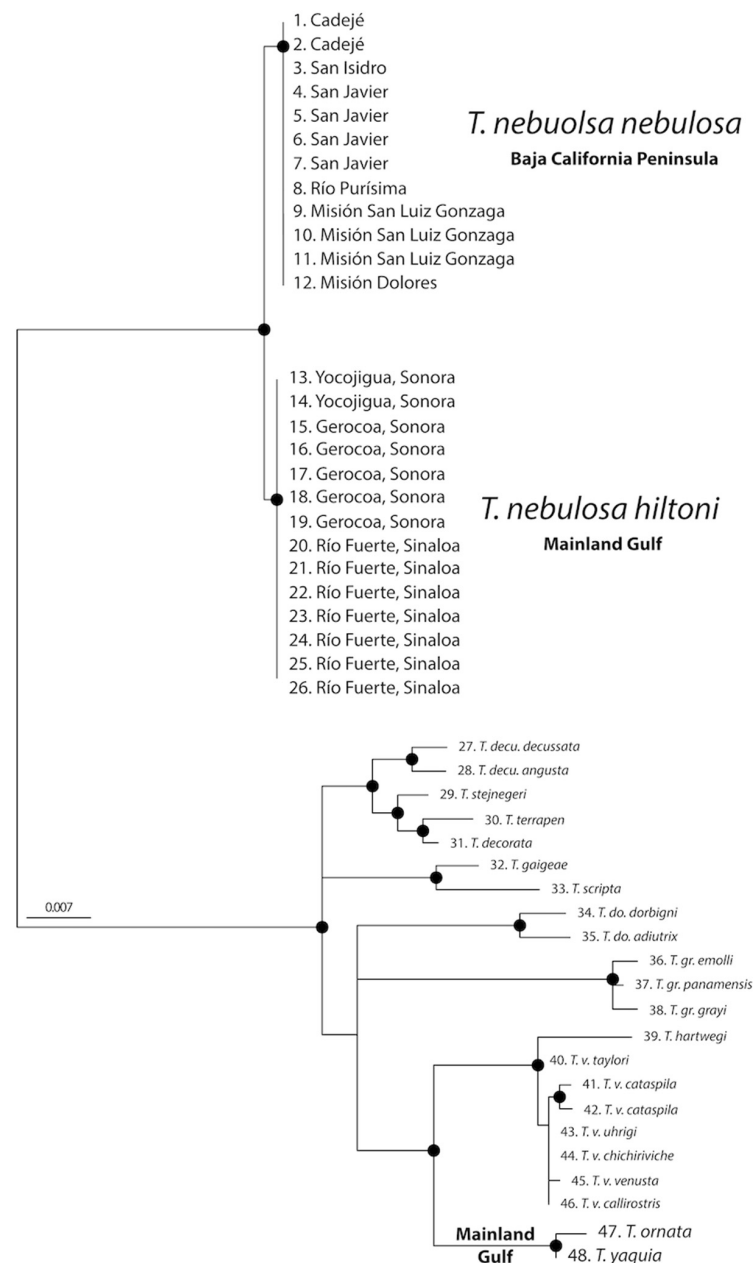


Figure 2. Maximum likelihood phylogeny based on a partitioned dataset of 884 aligned nucleotide characters of mitochondrial DNA from *Trachemys*. Black dots indicate nodes with bootstrap support ≥ 90 . Locality information is provided for *T. nebulosa*. Additional specimen, locality, and GenBank data are provided in the Supplementary Information (Table S1).

Newly generated and downloaded sequences of the three nuclear gene fragments were aligned as described above. Homologous R35 sequences of *Trachemys n. nebulosa* and *T. n. hiltoni* were downloaded from GenBank. A genetic network was constructed from the aligned dataset (3247 bp) to visualize patterns of genetic divergence using the Neighbor Net algorithm with p-distances implemented in SplitsTree App v. 6.7.8 (Institute for Bioinformatics and Medical Informatics, University of Tübingen, Tübingen, Germany) [35].

3. Results

The recovered mt tree is consistent with previous studies on the relationships of *Trachemys* (Figure 2) [11,12,21,36], including the previously recognized mtDNA discordance of *T. nebulosa* separating it from other *Trachemys*. Outside of *T. nebulosa*, the remaining sampled *Trachemys* taxa formed a separate clade. The other Gulf-associated taxa, *T. ornata* and *T. yaquia*, were nested deeply within that clade. All samples of *T. n. nebulosa* shared a single mt haplotype. Likewise, all samples of *T. n. hiltoni* shared a single haplotype distinct from the BCP haplotype. The divergence between the mt haplotypes of *T. nebulosa* subspecies is greater than that between some recognized subspecies of *T. venusta*.

The nu genetic network recovered two distinct groups corresponding to *Trachemys n. nebulosa* and *T. n. hiltoni* (Figure 3). The *T. n. nebulosa* cluster shows greater internal branching and haplotype diversity, whereas the *T. n. hiltoni* cluster is more linear and shows less divergence among samples. The two groups are separated by a relatively longer internal branch and lack reticulation between the subspecies. Overall divergence between the groups is shallow. The *T. n. nebulosa* samples have greater genetic coverage than the *T. n. hiltoni* samples, with 11 of 12 *T. n. nebulosa* individuals sampled for all three genetic markers, compared to just 7 of 14 *T. n. hiltoni* individuals. This difference in marker coverage may contribute to the stronger apparent genetic structure in *T. n. nebulosa*.

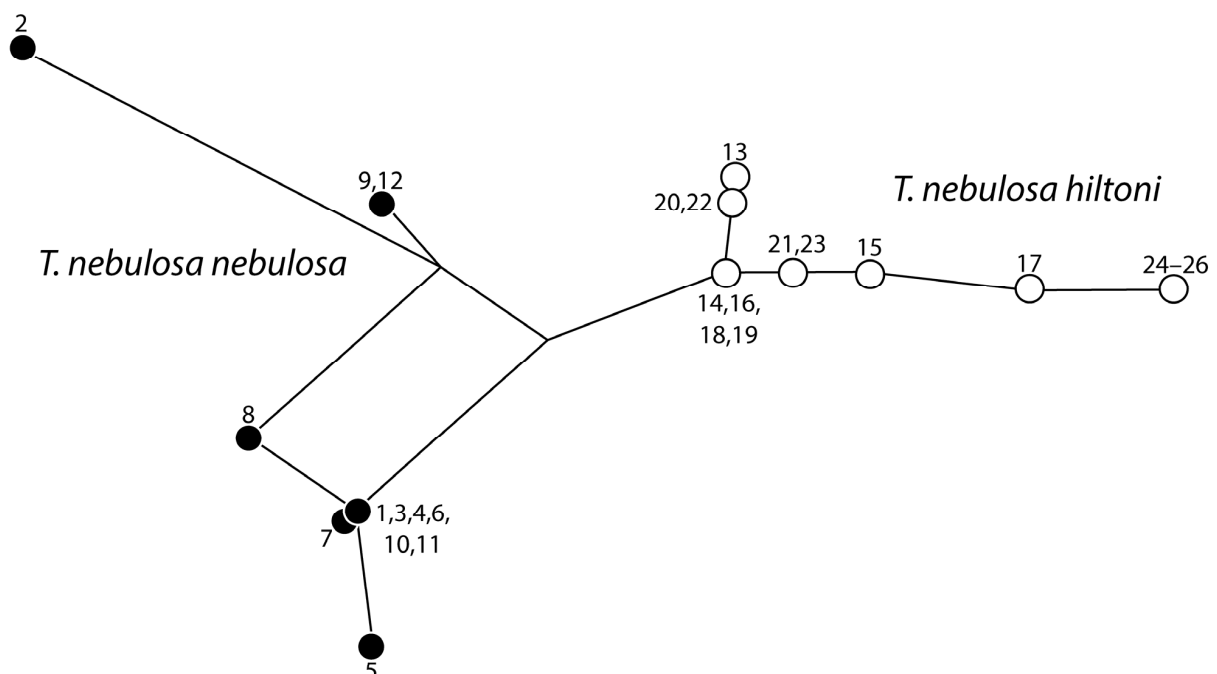


Figure 3. Genetic network based on 3247 aligned nucleotide characters of nuclear DNA from *Trachemys nebulosa*. Black circles represent haplotypes of *T. n. nebulosa* from the Baja California Peninsula, and white circles represent haplotypes of *T. n. hiltoni* from mainland Mexico. Numbers correspond to specimen or locality identifiers listed in the Supplementary Information (Table S1).

4. Discussion

Our samples of *T. nebulosa* from the BCP and the mainland do not share mitochondrial or nuclear sequences (Figures 2 and 3). Instead, both genomes recovered distinct genetic groupings corresponding to the two geographic regions. Although the genetic divergence between the two taxa is shallow, the differentiation supports a history of isolation predating human occupation of the Gulf region and is inconsistent with the hypothesis that either taxon represents a recent anthropogenic introduction [17,19–22]. The level of divergence also exceeds that observed among subspecies within the *Trachemys venusta* complex (Figure 2). Together, these results support the preliminary findings of previous authors [12,21] that *T. n. hiltoni* is distinct from *T. n. nebulosa*.

Trachemys n. nebulosa nuclear sequences from the BCP show somewhat greater internal branching and diversity than those from the mainland *T. n. hiltoni* populations (Figure 3), which is more consistent with the BCP representing the source region. However, this pattern should be interpreted cautiously because the BCP samples had more complete genetic coverage. Nevertheless, the deep mtDNA split between *T. nebulosa* and other *Trachemys* may also be consistent with a BCP-origin hypothesis, as it dates to the late Miocene and roughly coincides with the separation of the BCP from the mainland [21,37]. This pattern is complicated by the fact that the mt signal likely reflects an ancient capture event [21]. However, long-term isolation between *T. nebulosa* and other *Trachemys* species can still be inferred because parapatric populations in other *Trachemys* taxa typically show much shallower mt divergence and evidence of admixture [11,12,21,38]. For example, the *T. venusta* complex exhibits relatively limited mt differentiation despite it ranging from northeastern Mexico to South America [21]. This is also relevant to the geographic distribution of *T. n. hiltoni*, which intersects the distributions of *T. yaquia* and *T. ornata* on the mainland. The fact that *T. n. hiltoni* is morphologically and genetically distinct (Figures 1 and 2) is inconsistent with a simple mainland origin and instead suggests a more complex biogeographic history [12,21] (Figure 1). In this way, the distribution of *T. n. hiltoni* appears to interrupt the geographic pattern expected from phylogenetic relationships, making a later mainland arrival from the BCP more plausible. Although a BCP origin may seem unlikely given the arid conditions that characterize much of the peninsula today, the BCP experienced wetter conditions in the past, as indicated by other relictual oasis taxa (frogs, water snakes [17]) and a fossil record that includes more mesic-adapted species, including crocodylians [39].

A Baja California Peninsula origin for *T. n. hiltoni* would require overwater dispersal across the Gulf of California, but such dispersal may have been considerably more feasible during Pleistocene sea-level lowstands. Examples of natural overwater dispersal between the BCP and the mainland are uncommon among freshwater and terrestrial vertebrates [40,41]. However, during Pleistocene glacial lowstands, global sea level was approximately 100–150 m lower than today [42], exposing more of the Sinaloan coastal plain and substantially narrowing the marine barrier between the BCP and mainland. As a result, the minimum overwater crossing would have been reduced to less than 150 km. This distance is shorter than the overwater distances separating islands in the Antilles, where natural overwater dispersal has been proposed to explain the distribution of other *Trachemys* species [11].

Regardless of how the mainland populations of *T. nebulosa* became established, the continued recognition of *T. n. hiltoni* as a distinct evolutionary lineage underscores its conservation significance given its restricted range and harvest pressure [17]. The relatively low divergence between the two taxa and their subtle morphological differentiation suggest that additional work is needed before definitive taxonomic conclusions can be made. Expanded sampling in the Cape Region of the BCP will be important for verifying our

findings of genetic divergence between peninsular and mainland populations and the continued recognition of two taxa.

5. Conclusions

Mt and nu genetic data support the distinction between mainland and peninsular populations of *T. nebulosa*. The absence of shared sequences between the two regions argues against the anthropogenic introduction hypothesis suggested by most authors. Instead, the data suggest a longer history of isolation predating human occupation of the Gulf region. The available evidence is more consistent with a peninsular origin followed by natural dispersal to the mainland. Additional sampling from the Cape Region of the BCP will help clarify the history and taxonomy of these turtles.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d18070431/s1>, Table S1: Voucher information and GenBank accession numbers.

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Data Availability Statement: The data presented in this study are openly available in Genbank under accession numbers TBD–TBD.

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